"On the Nematocysts of Æolids." By G. H. Grosvenor, B.A., New College, Oxford. Communicated by Professor W. F. R. Weldon, F.R.S. Received November 3,—Read November 19, 1903.

While I was at Plymouth in July, 1902, Mr. W. Garstang suggested that I should investigate the origin of the nematocysts found in Æolids. He pointed out that no adequate account of their development had been published, and that the view held by some that they were derived from the Cœlenterate prey of the Æolids had never been properly tested. In looking up the literature of the subject, I came across Strethill Wright's abstract in the 'Microscopical Journal,' mentioned below, which convinced me of the advisability of a thorough examination of the question from this point of view before attempting to work out the development of the nematocysts in the Æolids themselves, especially as the few observations I had already made seemed to point in the same direction.

I. *Historical.*

The cnidophorous sacs at the apices of the cerata of Æolids were observed by Linnæus and O. F. Müller. Cuvier and Oken took them for suckers and Nordmann for mucous glands.

Alder and Hancock (1) were the first to observe the expulsion from these sacs of minute elliptical bodies provided with long hair-like tails. They noted a considerable resemblance to spermatozoa, but observed that there is no movement, and no apparent connection with the reproductive system.

These observations were continued by Hancock and Embleton (12), who give an accurate description of the "ovate vesicle," with its external opening and ciliated canal, communicating with the "liver cœcum." They also describe and figure the nematocysts of *E. papillosa*, *E. coronata*, and *E. olivacea*, and their disposition within the "ovate vesicle." They do not commit themselves to a definite opinion, but state that these bodies (the nematocysts) are "more like spermatozoa than anything else"; and they figure spermatozoa from the gonad for comparison, stating that the chief difference between the two are the more rounded body, and altogether inferior size of the latter.

By the time of writing the 'Monograph of British Nudibranchiata,' Alder and Hancock had arrived at a true conception of the nature of these bodies.

In December, 1858, T. Strethill Wright read a paper before the

Royal Physical Society of Edinburgh, in which he maintained that the cnidæ, or thread cells of the Æolidæ, were derived from the Hydroids on which they fed. He mentions that the same idea had previously occurred to Huxley and Gosse, and that the latter had suggested the method of proving its correctness. The observations which Wright brings forward in support of this view are as follows:—

1. An *E. nana*, found on a shell covered with Hydractinia, in a pool containing *Campanularia Johnstoni*, had nematocysts of two kinds found in Hydractinia, and also large distinct nematocysts of *C. Johnstoni.*
2. An *E. coronata*, found on *Coryne eximia*, contained nematocysts like those of the latter.
3. An *E. Landsburgii*, found on *Eudendrium rameum*, contained large bean-shaped nematocysts like those of the body of the polyps, and very minute ones, like those of the tentacles.
4. An *E. Drummondii*, found on *Tubularia indivisa*, had nematocysts of four kinds, found in the latter. Having fasted for "a long time," this specimen was fed on *Coryne eximia.* Next morning its papillæ and alimentary canal were crowded with the cnidæ of Coryne mixed with those of Tubularia.

He remarks that Joshua Alder was unconvinced, on account of the improbability of such a thing being true, and asks for further evidence.

In 1861 R. Bergh published a paper in Danish, which was abstracted in the 'Microscopical Journal,'* in which he described these organs in several species and genera in which they had not previously been observed. He considers them to be secreted in the cnidosac, and does not mention Strethill Wright's paper.

This omission induced Strethill Wright to publish in the next volume of the same journal an abstract of his former paper, in which he says that further observations and experiments had fully confirmed his view.

Owing either to the absence of figures, or to the afore-mentioned improbability of the conclusions it contained, this abstract seems to have been overlooked as completely as the original paper. I have not found a single reference to it in subsequent literature, and nearly all recent observers have taken for granted that the nematocysts develop within the Æolids themselves, and several have attempted to work out this development. Bergh has, indeed, mentioned in several places the possibility of a different view; for instance, in a footnote on p. 16 of 'Die Cladohepatischen Nudibranchien,' in reference to the frequent presence of more than one kind of nematocyst in the same individual, he says: "Es ist noch fraglich ob nur eine Art Cnidæ in

* Vol. 2, 2nd ser.

den Nesselsäcken gebildet wird, und ob die anderen von der Höhle der Leberlappen herrühren, von verzehrten Thieren." On the same page he states that "ganz eigenthümliche, grössere Formen" (of nematocysts) are found in several genera (Glaucus, Coryphella, Flabellina, Pterœolis).

Herdman and Clubb (1889), and Herdman (1890), placed beyond doubt, by means of serial sections, the existence of a ciliated canal connecting the cnidosac with the "hepatic" diverticulum. This had, apparently, been doubted by many,* though I think conclusive evidence on the point may be found in several previous papers by Bergh and Trinchese, not to mention Hancock and Embleton.

In the second paper Herdman states that the cnidosac is "evidently of ectodermal origin." Probably the presence of such typically ectodermal organs as nematocysts was one of the chief reasons of this assertion.

Davenport proved by tracing the actual development that the cnidosac arises not from the ectoderm, but from the distal extremity of the gastric diverticulum. This has since been confirmed by Hecht and Krembzow.

The last four authors have all described and figured what they took to be young stages in the development of the nematocysts, and Hecht and Krembzow have attempted to trace this development in detail. The former considers the nucleus to take a prominent part either by "directing" the secretion of nematocysts by the cytoplasm, or, as he thinks, more probably by giving up a portion of its substance to form the rudiment of the nematocyst. But Krembzow points out that in many cases the cnidoblast is elongated, the nucleus lying at the basal end, while the nematocysts occur from the first at the end next the lumen of the cnidosac.

Most of the other observations which I have found bearing on this question are scattered through works dealing with the general anatomy and classification of the group, and will be more conveniently mentioned later on.

Quite recently, however, since a rough draft of the present paper was already written, a note appeared in the Johns Hopkins 'University Circular' by C. O. Glaser, in which the writer brings forward and discusses the view that the nematocysts of Æolids are extraneous and derived from their prey. After pointing out that many Æolids are found in association with hydroids or actinians, and that Alder and Hancock observed fragments of a hydroid in the alimentary canal of an Æolid, he shows that the present accounts of the development of nematocysts are unsatisfactory, and that the appearance of nematocysts in endodermal cells, and apparently independent of the nucleus, is at least unexpected. He then records three observations of his own in support of this view—

* See Lankester's "Mollusca," 'Encycl. Brit.,' 9th edit.

1. An *E. alba*, found on a colony of Paripha, had nematocysts of two kinds, indistinguishable from those of the hydroid.
2. An *E. rufibranchialis*, found on Eudendrium, had nematocysts about one-third the size of those of *E. alba*. These were apparently not compared with those of Eudendrium; at any rate the result of the comparison is not given.
3. A young *E. alba* was found in a large vessel of sea water in which various marine larvæ were being reared. This Æolis must have been over 2 months without hydroid food and had probably metamorphosed in the vessel. It had no nematocysts.

Having discussed one or two difficulties, the writer concludes that further investigation of this point is desirable, and that it may turn out that nematocysts are not "part of the organic make-up" of the Æolidæ. He is apparently unaware of Strethill Wright's work.

II. *The Nematocysts of Æolids are derived from their Cœlenterate Prey.*

Before describing my experiments, which, I think, afford conclusive confirmation of Strethill Wright's view, I shall proceed to discuss a number of facts which have come under my own observation, or which I have collected from the literature of the group, which point in the same direction and would, indeed, be sufficient by themselves to prove the truth of this view.

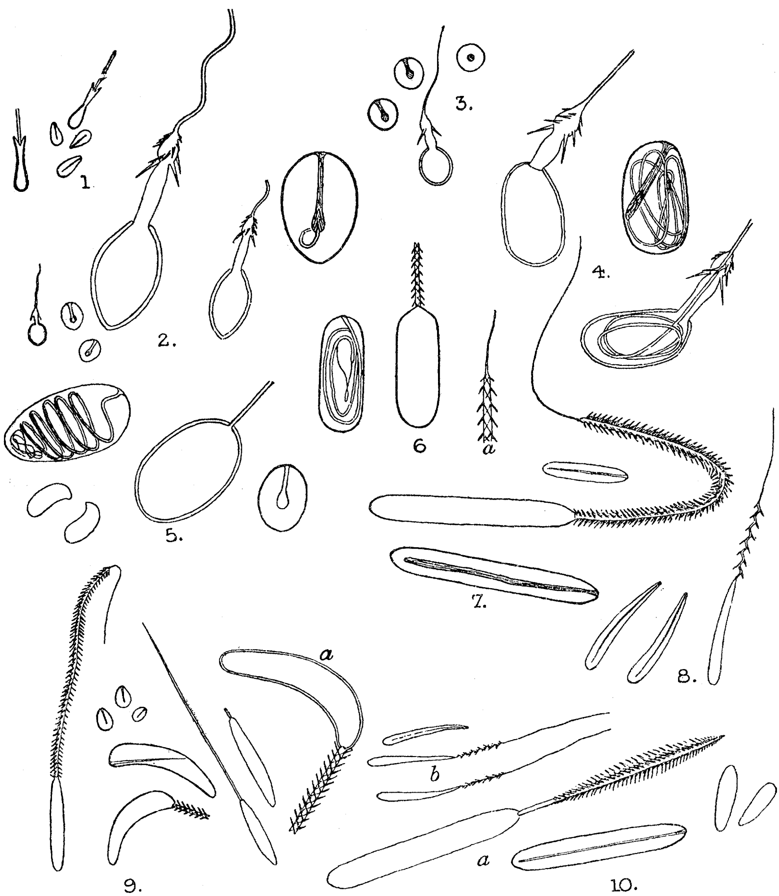
1. Great Similarily of the Nematocysts of Æolidæ and Cœlenterates:

I think that those who quote the nematocysts of Nudibranchs and Cœlenterates as a striking example of homoplasy or convergence, can scarcely be aware of the astonishing completeness of this assumed convergence. It is not simply a case of nematocysts of the same general plan occurring in the two groups, but of each of several distinct forms of nematocysts being found in both groups. For instance, the most characteristic Actinian nematocysts have elongated semi-cylindrical capsules; they are either straight, varying from 20—60 μ in length, with the basal portion of the thread (twice the length of the capsule) thick, and closely covered with long fine bristles (fig. 7); or the capsule is slightly curved, about 25 μ in length, and narrower in proportion than in the last form, while the thread is uniformly tapering, slightly spiral, and furnished with short relatively stout barbs for a distance rather less than the length of the capsule (fig. 8). Both these forms are of frequent occurrence in Æolids belonging to Bergh's sub-family *Aeolidiadæ propriæ*.

Small nematocysts, 8 μ or less in length, shaped something like an apple pip (fig. 1), are very widespread in the hydroidea; they occur,

with slight variations in actual size and in relative breadth, in Eudendrium, Gonothyrea, Obelia, Sertularia, Sertularella, Antennularia, Plumularia, &c.; they are also, perhaps, the most common form in Æolids, as may be seen from a glance at the plates in Bergh's "Beiträge zur Kenntniss der Aeolidiadæ," or Vayssière's "Opisthobranches du Golfe

FIGS. 1—10.



de Marseille." I myself have found them in the following genera:—Rizzolia, Calma, Flabellina, Coryphella, Amphorina, Facelina, Galvina.

Rather small spherical nematocysts, very like those of Hydra, are found in Tubularia and other marine hydroids. I have found them in Rizzolia, Coryphella, Facelina, and Cuthona (fig. 3).

These facts are in no better accord with the idea of genetic relation-

ship,* for nothing short of the polyphyletic origin of Æolids from diverse Cœlenterates would bring us any nearer an explanation.

2. Nematocysts of different types occurring in individuals of the same species, or in the same individual.

The following instances will illustrate this:—

i. Of 48 *R. peregrina*, while all had small pyriform nematocysts (fig. 1),
  - (*a*) 20 had no others,
  - (*b*) 16 had also large bean-shaped nematocysts, like those of Eudendrium (fig. 4),
  - (*c*) 10 had both these, and also small round Tubularia-like nematocysts (fig. 3),
  - (*d*) 1 had only small pyriform and small round nematocysts,
  - (*e*) 1 all the forms found in (*c*), and in addition a few similar to those shown in fig. 6, but about half the size.

ii. Of 29 specimens of *Spurilla neapolitana*, 26 (including 4 young specimens from 1·5—2 cm. long) had nematocysts shown in fig. 8; three very young specimens (less than 1 cm. long.) had nematocysts like those in fig. 9. This may, perhaps, indicate that a change of food is a regular occurrence in the life-history of this species.

iii. Of two young specimens of *Facelina punctata*, one had nematocysts of at least five different kinds, shown in figs. 1, 3 and 5; the other had nematocysts of two kinds indistinguishable from those of *Pennaria Cavolinii* (see below), (fig. 2).

Such individual variations have often been noticed by writers on this group, and in his recent paper on the development of the cerata, Krembzow remarks on such a case in *Aeolidiella glauca*, one of his specimens having a different type of nematocysts from the others; he seems almost inclined to consider it a different species on this account, though after a careful examination he was unable to discover any other difference, anatomical or histological.

I imagine that what uniformity in this respect does exist (and this must be considerable in the majority of species, or the idea of the development of nematocysts within the Æolids would never have endured so long), must be due to a decided preference on the part of each species of Æolid for a particular kind of hydroid, for living and feeding on which they are specially adapted. In this connection the case of *Flabellina affinis* and *Coryphella Lansburgii* is interesting. These species are by no means nearly related, being placed by Bergh in separate sub-families. But in external appearance they show a remarkable resemblance. The specimens I have examined show

* *Vide* Lankester's 'Treatise of Zoology,' Part IV, p. 12.

approximately the same range of variation in size; the colour in both is a beautiful translucent violet, with brick-red or carmine diverticula of the gastric gland showing through the integments of the cerata. I have no direct evidence as to what hydroids they frequent, but I have on several occasions received specimens of the two species together, and the evidence of their nematocysts given in the following table, leaves no doubt that their food is the same. This is probably, therefore, a case of mutual mimicry, since both species are protected (by mucous glands and nematocysts).

	Small pyriform nematocysts and large bean-shaped nematocysts of Eudendrium.	Small pyriform and large oblong nematocyst (fig. 6).	All three kinds.	Total.
Flabellina affinis........	2	4	2	8
Coryphella Landsburgii..	3	4	2	9

The nematocysts figured in fig. 6 I have not as yet been able to find in any Cœlenterate; they are apparently those which Bergh considers "ganz eigenthümliche." But I think the evidence is scarcely in favour of this view, even when this case is considered by itself. For, as shown above, these nematocysts are found in about half of each of these by no means nearly related species; while, on the other hand, I could not find a trace of them in two specimens of *Cor. Scacchiana* or five *Cor. lineata*. I have not had an opportunity of examining any other species of Flabellina.

3. Whenever it is known what particular Cœlenterate an Æolid has been feeding on, the nematocysts of the two are found to be identical.

Strethill Wright gave four instances of this and Glaser has given another. I may add a few more.

As mentioned above, the *Æolidiadæ propriæ* of Bergh have usually typical Actinian nematocysts, and many of them are known to feed on Actinians. An *Ae. papillosa* found at Plymouth among stones on which the common red Anemone was abundant, had nematocysts indistinguishable from the latter. An *Æolidiella Alderi* dredged at Plymouth had nematocysts exactly like those of Sagartia (fig. 6). It is known to feed on a species of Sagartia (see Garstang (9)). Mr. Garstang told me that he had been struck by the similarity of the nematocysts of these two animals some years ago, and showed me drawings he had made at the time.

Also two *Amphorina cœrulea* found on Sertularella; a Facelina sp. found on Antennularia; a *Cuthona aurantiaca* and three *Facelina coronata* on Tubularia; *Facelina punctata* on *Pennaria Cavolinii*; three *Rizzolia peregrina* dredged with *Eudendrium rameum*; four *Rizzolia peregrina* dredged with Eudendrium sp.; all had nematocysts indistinguishable from those of the hydroid with or on which they were found.

But it is possible in many cases where the "food hydroid" of an Æolid is unknown, to prove that the nematocysts in the cnidosacs of the Æolid are the same as those of its prey, whatever that prey may be; for it has been noted by several observers (Alder and Hancock, Hecht, &c.) that the fæces of Æolids consist largely of nematocysts, obviously derived from their food, but no one seems to have compared them with those found in the cnidosacs. I have made this comparison in a number of cases, and have always found the nematocysts in the fæces identical with one or more forms which occur in the cnidosac. In those individuals which have many different types of nematocysts in their cnidosac, these are not always all represented in the fæces, for the latter are extruded a day or two at most after the meal of which they are the remains, while nematocysts may remain in the cnidosacs for at least a month, as is proved by an experiment to be described presently.

4. Those Æolids which are known to feed on animals unprovided with nematocysts have no nematocysts themselves:

Thus the sub-family Janidæ, many of which are known to feed on Polyzoa (see Garstang (9) and Giard (10)), have no nematocysts. Since these forms have also no cnidophores and in many other ways are very aberrant, it might be objected that they branched off from the Æolid stem before the acquisition of nematocysts by the latter, and the fact of their feeding on Polyzoa was a mere "coincidence." This objection, however, cannot apply to the case of *Calma glaucoides*. This is in all other respects a typical Æolid, but, according to M. Hecht (1), it has no nematocyst and no cnidosacs. According to the same author there can be no doubt that the food of this species consists of the eggs and embryos of various shore fish (Cotta, &c.). The only other member of the genus Calma is *C. Cavolinii*, which has typical cnidophores, usually crowded with nematocysts, and which feeds on hydroids, for I have found unmistakable fragments of the same in the stomachs of several specimens, as well as nematocysts in the fæces.

M. Hecht, seeking an interpretation of the coincidence of non-cœlenterate food and absence of nematocysts in *C. glaucoides*, in the light of the current opinion as to the origin of nematocysts in Nudibranchs, writes as follows: "On peut considérer l'absence de sacs à nematocystes chez *C. glaucoides* comme un pur phenomène de dégénérescence, étant donné qu'ils existent chez une espèce voisine; quant à

la cause, elle est difficile à pénétrer. On sait que les Æolidiens se nourrissent fréquemment de Cœlentérés (Hydraires, Actinies), et paraissent doués d'immunité vis-à-vis de leur nématocystes; or il est curieux de se remarquer que c'est précisément une espèce qui ne s'attaque pas à des Cœlentérés, qui est dépourvue de sacs cnidophores."

We see from this case that the degeneration and atrophy of the cnidosacs follows very soon the abandonment of a Cœlenterate diet.

Fiona is another genus unprovided with cnidosacs. I have not been able to find any record of the food of this genus, but Dr. Lo Bianco tells me that about 3 years ago large numbers of *Fiona nobilis*, Velella and Janthina, were taken together in the Bay of Naples, and that he observed the Fionæ feeding on Velella, the individuals which had so fed being coloured a deep blue. Velella and Fiona were also taken this spring in company, and I observed Fiona devouring the siphonophore; a normally coloured Fiona becomes blue very soon after feeding on Velella and its gastric diverticula become crowded with nematocysts. The blue colour persists for a considerable time (a week to 10 days) without a further supply of Velella, so that if this was the staple food of this species, we should expect the majority to be blue, which is not the case. Besides those taken with Velella, a number of *Fiona nobilis* were found on floating pieces of pumice or wood covered with a species of Lepas. I kept one such colony in a large jar of sea-water, and next morning the bodies of half-a-dozen barnacles were lying on the bottom, their stalks having disappeared. As the remaining barnacles were quite healthy, I think there can be no doubt that the stalks had been devoured by the Nudibranchs. It seems probable, therefore, that the food of Fiona is varied, and that the proportion of Cœlenterates is not sufficient to give a constant supply of nematocysts, so that the cnidosacs have been lost or never developed.

5. The inadequacy of the published accounts of the development of nematocysts in Æolids is remarked on by Glaser, who also points out that even if undoubted developmental stages were found, it would not prove that they arose in the Æolid, for they might well be introduced together with the fully formed ones. The comparative scarcity of young stages (I myself have never found anything which I could confidently affirm to be such) I take to be due to the following causes:—

(1) The development of nematocysts in the less accessible basal part of the polyp and their migration only when fully formed to the exposed positions where they are of use.

(2) The greater digestibility of the young stages. Spirocysts must also be digestible, for though they are as numerous as nematocysts in many Actinians, they are not found in actinian-eating Æolids. But Bedot states that he has found them in Pleurophyllidia (3).

6. The Ciliated Canal between the Gastric Diverticula and Cnidosac :—

The existence of this canal, as mentioned above, was first established in transparent pupillæ by Hancock and Embleton, and subsequently by means of serial sections by Herdman and Clubb and others; but its function has always remained a mystery. Hecht suggested that it might act as a safety valve, to allow the escape of superfluous nematocysts from the cnidosac. Krembzow combats this view and maintains that the function of the canal is to allow the passage into the cnidosac of nematocysts developed in the "liver cells." Though there is no better evidence for the development of cnidæ in the "liver" than there is for their development in the cnidosacs, this view is certainly more in accordance with observed facts than the former. For as Hancock and Embleton observe, the cilia on the walls of the canal cause a current towards the cnidosac; these naturalists also note that particles of various sorts, "accidentally pressed into the canal," are carried into the cnidosac. Trinchese (1) actually observed the passage of nematocysts in this way,* but, like Hancock and Embleton, he considered this a purely artificial effect. He notes that the cnidæ so passing are sometimes like those already in the cnidosac, sometimes different, and remarks: "In ambo i casi esse appartevano ad individui mangiati dal suddetto animale (Facelina sp.); nel primo caso esse appartevano a qualche Facelina, nel secondo ad Æolididae di altri generi." It is curious that he does not consider the possibility of their derivation from Cœlenterate prey. I have also observed the passage of nematocysts through the canal, and certainly in this case they belonged to a hydroid (*Pen. Cavolinii*) devoured a short time before.

The ciliated canals and cnidosacs have of course no power of distinguishing nematocysts from other small indigestible bodies. Thus Hecht observed that when some *Facelina coronata* had been feeding on Elysia, the radular teeth of the latter appeared in the cnidosacs of the Facelina. I have observed the same thing in the case of *F. Drummondii* which had devoured two small specimens of *R. peregrina.* Probably the bâtonnets mentioned by Vayssière as occurring in the cnidosacs of *Flabellina affinis* and other species of Æolids,† are due to the individuals in question having varied their diet by devouring some spiculiferous organism.

Experiments.—Strethill Wright's most conclusive evidence for the extraneous origin of nematocysts in Æolidæ was his experiment of feeding an *E.* (*Facelina*) *Drummondii*, having Tubularia nematocysts in its cnidosacs, on *Campanularia Johnstoni*, the nematocysts of which subsequently appeared in the cerata of the Æolid. I have carried out similar experiments on a number of individuals of two species of Æolids,

* Part II, p. 53.

† *Loc. cit.*, p. 82.

Rizzolia peregrina and *Spurilla neapolitana*, which are the species most easily obtained in the late autumn at Naples.

1. Four specimens of *Rizzolia peregrina* were obtained at the beginning of November, being dredged with some tufts of Eudendrium. These had nematocysts of one kind only, which were small (average length 6·5 μ), pyriform or pip-shaped, and are shown in fig. 1. These specimens were placed in a small aquarium with several colonies of *Pennaria Cavolinii.* The nematocysts of this hydroid are of two kinds, which differ chiefly in size, the larger being about 25 μ, the smaller 7 μ, in length. They are oval, and slightly pointed at the end of the capsule opposite the base of thread (fig. 2). It will be seen that these could not possibly be confused with the nematocysts found in the cnidosacs of the Æolids at the time of capture.

For some days the Nudibranchs were too much occupied in depositing eggs to pay any attention to the unaccustomed food provided for them, but on the ninth morning I noticed that several branches of the hydroid were denuded of polyps, and, on examining the cerata of the Æolids, I found a considerable number of Pennaria nematocysts mixed with the original ones, which were still preponderant in numbers.

Remembering Bergh's opinion, that one kind of nematocyst is developed in the cnidosac, while others may be derived from hydroids, I continued to feed these individuals on *P. Cavolinii* for a month. At the end of this time the original nematocysts were almost entirely replaced by those of Pennaria; in some papillæ I could not find any but the latter, and in none that I examined did the small pyriform cnidæ amount to more than 2 per cent. of the total number in the cnidosac.

2. Four other specimens of *R. peregrina* were kept in an aquarium with Eudendrium, Pennaria, Tubularia, and *Aiptasia variabilis.* These specimens had at capture nematocysts of two kinds found in some species of Eudendrium; the small pyriform kind is shown in fig. 1 (occurring on the tentacles of the hydroid), and large bean-shaped ones, shown in fig. 3 (found in a definite zone on the body of the polyp). After a month in the aquarium they had, of course, still a number of Eudendrium nematocysts, since this hydroid was included in their food; but they had also a considerable number of Pennaria and Tubularia nematocysts, and a few from the acontia of Aiptasia, though the latter is very different from their accustomed prey, and, in fact, *R. peregrina* does not seem adapted to attack Actinians (see below). Besides these there were a few oval nematocysts, with a considerable length at the base of the thread, covered with fine barbs, which must have been derived from a small hydroid inadvertently introduced with the others, and which I have not been able to identify; they certainly cannot be the nematocysts developed in *R. peregrina*, since they only

occurred in two of these specimens, and in none of the other fifty I have examined.

3. Two specimens of *R. peregrina* were placed in a large jar of sea-water, with two amputated probosces of *Cerebratulus urticans.* They did not take kindly to the diet, but, after several days, one had eaten sufficient to fill its cnidophores with an inextricable tangle of the long sinuous nematocysts of the nemertine, while the other had a few of the same both in the cnidophores and in the "hepatic" diverticula.

4. Two specimens of *Spurilla neapolitana,* which had nematocysts of one sort only shown in fig. 8, were fed on *Aiptasia variabilis,* which has two kinds of nematocysts, shown in fig. 7; the cnidosacs of the Æolids soon became crowded with the nematocysts of Aiptasia (especially those of the acontia), but I was not able to continue the experiment long enough to entirely replace the original form. Besides the two forms of nematocysts mentioned, Aiptasia has a large number of small spirocysts. These have a much more fragile appearance than true nematocysts, and they must be destroyed and digested by the gastric fluids of the Æolids, for I could not find any in the cnidophores of these two specimens.

In all these cases the nematocysts newly introduced did not simply lie free in the lumen of the cnidosac, but were included in "cnidoblasts" in the same way as those present in the Æolids at capture (fig. 12).

III. *Function of Nematocysts and Cnidophores of Æolids.*

If it is allowed that the nematocysts found in the cnidosacs of Æolids are of extraneous origin, and, in fact, are *quasi fæcal* products of the digestion of cœlenterate prey, the question arises, "Is the elimination of these inconvenient, and possibly dangerous constituents of the food, the sole function of the cnidosacs and their associated mechanism, or do they also serve as a means of offence or defence"? The difficulty of believing that the Æolid uses for its own purposes the very weapons presumably "intended" to defend the hydroid from the Æolid and other enemies, seems to have been the chief cause of Alder's scepticism in regard to Strethill Wright's results. The nearest parallel I know of is the case of the Cephalopod *Tremoctopus microstoma,* described by Troschel, and later by Joubin, as possessing nematocysts borne on special cylinders on the arm. M. Bedot has proved by sections that these cylinders are nothing more nor less than fragments of the arms of a Medusa, and he remarks: "Nous avons, donc, ici un exemple intéressant d'un animal empruntant pour sa défense les armes d'un autre animal, caractère considéré habituellement comme étant l'apanage exclusif de l'homme." In this case, however, direct evidence of the use of the nematocysts seems entirely wanting, and it is only the regular

occurrence of these cylinders which leads one to suppose they must serve some useful end. Certainly, the evidence of the use by the Æolids of their stolen nematocysts is very much stronger.

In the first place, the nematocysts discharge themselves, after extrusion from the cnidosac. I mention this, because the fact might be considered improbable, though it has been recorded by many observers. It is true that, in many cases, the cnidæ are so minute, and the discharge is effected with such rapidity that the act itself is difficult or impossible to follow. But tips of the cerata are so transparent that the cnidæ can usually be seen lying in the walls of the cnidosac undischarged; whereas a second or two after they have been extruded into sea water, the threads of the majority are everted. Sometimes the actual eversion itself can be seen, as when the thread is very conspicuous (*e.g.*, large Actinian nematocysts) or when, for some reason, the eversion takes place slowly. For instance, I have seen the large bean-shaped nematocysts of Eudendrium from a ceras of *R. peregrina* evert the distal portions of their threads with great deliberation; the part already everted lengthened with a curious sinuous motion of the tip, while the part still within the capsule uncoiled itself at a corresponding rate. (I need hardly say that I cannot confirm M. Hecht's opinion that the nematocysts of Nudibranchs differ from those of Cnidaria, in that only the basal portion of the thread of the power is inverted, the distal part being coiled up inside the inverted base; on the contrary, in all cases, in both Nudibranchs and Cnidaria, in which I could clearly distinguish the thread inside the capsule, it was coiled up more or less regularly, between the inverted base and the wall of the capsule, and must, therefore, have been inverted itself.)

The arrangement of the nematocysts within the cnidosac seems to indicate that they are used as weapons, for they usually lie with the aperture, through which the thread will be everted, turned towards the periphery of the "cnidoblast." It is true that the round Tubularia-like nematocysts lie much more indiscrimately, and that even the long Actinian nematocysts are sometimes reversed, but as a general rule the arrangement is as described.

The fact that those species which have no cnidosacs are more richly provided with glands on the cerata, as if in compensation for their absence (see Hecht on *Calma glaucoïdes* and Krembzow on Fiona), seems to point to the same conclusion.

But if the nematocysts are used as weapons, they may be either—

1. Offensive weapons, used against prey,
2. Defensive weapons, used against enemies.

1. This view was suggested by Bergh in his paper of 1861 (according to the abstract in the 'Microscopical Journal'). But I have often watched Æolids feeding, and noticed that the cerata are held in the normal

position, directed backwards along the sides of the body; moreover, it is doubtful whether the nematocysts which, in the ordinary course of events, would have been derived from the very species being devoured, would be very effective for paralysing the same.

2. The second alternative is the one most generally accepted, and I think it is undoubtedly the correct one. The experiments of Herdman and of Garstang prove that Æolids are unpalatable to many fish (apparently not to all, for McIntosh states that the cod eats *Æolis papillosa*, but according to the same authority the most deadly bait for cod are bright coloured anemones, and young flat fish fill their stomachs with Edwardsia; so that for these fish nematocysts evidently have no terrors). No one can have witnessed the reaction of an Æolid to various stimuli (touch of a foreign body, agitation of the water or, in some cases, a shadow), without being convinced that the cerata are used as a means of defence. The body is contracted, the head being often nearly telescoped into the trunk, while the cerata are erected and waved about, especially in the direction of the foreign body, and are often considerably extended (in *R. peregrina* the cerata when excited are nearly double their length when at rest).

But though the nematocysts are undoubtedly used defensively, I think the actual method employed is generally misunderstood. The Æolid is often described as "threatening" the foreign body with its cerata, the supposition being that nematocysts are shot out against it. It is certainly true, as stated above, that the cerata are turned towards the foreign body which has touched the animal, but in experiments on upwards of 40 individuals I have never seen nematocysts extruded under these circumstances; and the mass of nematocysts extruded from a cnidosac is quite visible to the naked eye. I have, indeed, only once witnessed the emission of nematocysts for cerata still attached to the body of an Æolid, and not themselves individually squeezed or otherwise ill-treated. On this occasion a *Sp. neapolitana* about 3·5 cm. in length, in a small beaker of sea-water, was somewhat violently stimulated with a glass tube. It erected its papillæ, which in this species are very numerous and usually carried curled up along the sides of the body, and lashed them about in all directions, at the same time emitting quite conspicuous little masses of nematocysts from its cnidosacs. These were carried by the currents in the water and adhered as a flaky white deposit to the bottom of the vessel. On examination they were found to consist almost entirely of discharged nematocysts. It is, I think exceedingly doubtful whether this promiscuous discharge would have much effect on such an enemy as a fish, for

(1) A very small proportion of nematocysts would come in contact with the fish,

(2) Since eversion of the thread follows, as a rule, very rapidly on

the extrusion from the cnidosac, the few that did reach the fish would probably be already discharged,

(3) It is very doubtful whether nematocysts would penetrate the scaly covering of a fish large enough to be dangerous to an Æolid.

It is, therefore, not surprising that this method of defence is not more generally employed.

With this single exception, in all the Æolids with which I experimented nematocysts were emitted only when individual cerata were squeezed or plucked off. In this way a fish which had snapped at the cerata, the loss of which, as is well known, does not seem to inconvenience the Nudibranchs at all, would receive a discharge of nematocysts into its mouth, where they would probably act with the greatest possible effect. This is in complete agreement with Garstang's view as to the meaning of certain features in the coloration of Æolids. He suggests that the localisation of the bright colours in the cerata "serves to direct the experimental attacks of young and inexperienced enemies to the non-vital papillæ and away from the vital and inconspicuously coloured parts of the body," and "at the same time gives them (the enemies) the needful experience of the unpalatable nature of their intended prey" ((9) p. 175). The erection and elongation of the cerata conduce to the same result (*i.e.*, make them the most probable mouthful for an enemy), even when the bright colours are absent or otherwise disposed.

But though the nematocysts are certainly used as defensive weapons, their removal from the digestive system is an important, perhaps the original, function of the cnidosacs. In molluscs other than the cladohepatic Nudibranchs, the food is digested in the stomach, the liquefied products being passed into the gastric gland, where absorption takes place (see Simroth (20)). In Tritonia, therefore, the anus suffices for the passage of nematocysts out of the body. But in the Cladohepatica part of the food is digested in the gastric gland, quite fresh pieces of hydroid being found in the ducts and ceratal diverticula of a recently fed Æolid. On examining the cerata of a Doto which had been feeding on *Pennaria Cavolinii*, I found them crowded with large nematocysts. How Dotonids, which habitually feed on hydroids and have no apertures in their cerata, get rid of the nematocysts I cannot say; perhaps by throwing off their cerata, which as is well known they do with great ease. When an aperture for the extrusion of nematocysts had once been acquired, it would be obviously advantageous that the distal end of the "hepatic" diverticulum should be modified to form a cnidosac where the nematocysts might be stored to be used in defence as required.

IV. *The Mechanism of the Discharge of Nematocysts.*

To understand how an Æolid is able to swallow Cœlenterate nematocysts undischarged, pass them in this condition through its alimentary canal, and then discharge them in its own defence, we must know something of the conditions and causes of this discharge. As far as I know, this question has never been discussed as regards Nudibranchs, but the theories brought forward to explain the action of the nematocysts in Cœlenterates are innumerable. In 1887 von Lendenfeld considered the solution of the problem in sight; but ten years later he confesses that the increase of knowledge has only multiplied hypotheses, and an adequate explanation seems further off than ever. I think a consideration of the behaviour of nematocysts in Æolids throws some light on the question.

When nematocysts are extruded from a cnidosac and subsequently evert their threads, not only have the original Cœlenterate nematocytes been digested, but the nematocysts are often quite free from any trace of protoplasmic substance, even the "cnidoblast" in which it was contained in the cnidosac. The discharge, therefore, cannot be directly due to the contraction of the nematocytes or surrounding tissues of the Cœlenterate.

Nussbaum and others have suggested that the elasticity and tension of the capsule itself aids in causing the eversion of thread, while Grenacher considers this tension sufficient in itself to evert the thread but for the resistance of the operculum ("Deckelchen") covering the opening; any slight access of pressure from outside suffices to overcome this resistance and causes the discharge. But in this case the nematocysts would be at least as likely to be discharged while being swallowed by the Æolid, as when lying undisturbed in the sea water after extrusion from the cnidosacs.

The theories so far discussed rely on the assertions of H. Frey, Clarke, Gräffe, and others that the capsule of a nematocyst is smaller after than before discharge. Iwanzoff, on the other hand, from a series of measurements and calculations, reaches the conclusion that while the capsule itself may be smaller, the total capacity of the nematocyst is larger after discharge. For in a resting nematocyst the volume of the thread must be subtracted from that of the capsule; while in a discharged nematocyst, the thread being hollow, its capacity must be added to that of the capsule. The substance contained in the capsule has therefore increased in volume, and Iwanzoff considers this to be the cause of the eversion of the thread. He supposes the original contents of the nematocyst to consist of a highly hygroscopic gelatinous substance; this is protected from the access of water by the impervious capsule wall and the operculum over the aperture of the inverted thread. When this operculum is removed by the action of the

nematocytes or other cells, and the nematocyst itself is thrust out into the water, the latter enters the basal portion of the inverted thread, diffuses through its thin walls and causes the gelatinous substance to swell up. He mentions in support of this the staining properties of the nematocyst contents; this, when undiluted, *i.e.*, in an undischarged nematocyst, stains darkly with picric acid or methylen blue; in successive stages of the eversion of the thread it stains successively lighter.

Von Lendenfeld, in reviewing this explanation of Iwanzoff's, says: "So schön diese Theorie auch ist, so erscheint sie doch ganz unhaltbar," the objections which he considers insurmountable being two:

1. The thin probably chitinous wall of the capsule could not possibly prevent the access of water to the intensely hygroscopic contents.
2. The fact that the contents of undischarged nematocysts are stained proves that water can enter without discharging them.

Also when a nematocyst is extruded from a cnidosac of an Æolid, as stated above, there is nothing there capable of removing the operculum. But, though the second objection seems fatal to Iwanzoff's theory as it stands, I think a slight modification of the same will not only avoid these difficulties but explain a number of facts inexplicable on any other hypothesis as yet propounded.

When we examine the conditions antecedent to the discharge of nematocysts in Cœlenterates and Nudibranchs, we find that apparently the only one common to the two cases is a change of the medium immediately surrounding the nematocyst. In Cœlenterates the nematocysts before discharge are partially protruded from the surface of the nematocytes into the surrounding water; in Æolids the nematocyst is extruded from the cnidosac into the water. The nematocysts of the fæces also discharge themselves on being extruded from the rectum into water. In each case it seems to be the passage from a solution of greater to one of less concentration which causes the eversion of the thread. This idea is confirmed by the following observations:—

1. In connection with the earlier part of this paper I had occasion to examine a large number of Æolid cerata for the identification and comparison of the nematocysts. For this purpose I found Calberla's fluid a very convenient examination medium; but though large numbers of nematocysts were usually extruded on placing the ceras in this liquid, the threads were never everted except when a large proportional amount of sea water was carried over with the ceras.
2. Similarly, if a ceras be examined in a fairly strong solution of sugar or salt, the nematocysts are not discharged, but if the

preparation be subsequently washed out with distilled water, the threads of the nematocysts are at once everted.

3. I have obtained similar results with Actinian tentacles. If a tentacle of an expanded Actinian is plucked off and plunged as quickly as possible into a 50-per-cent. concentrated solution of sugar, and then teased up, though many nematocysts are found discharged, it is quite easy to find pieces in which none are discharged. I have isolated such pieces, and after further teasing up, have kept them for periods varying from 24—72 hours. The nematocysts were always still undischarged, but when the sugar solution was washed out with water a certain number (never more than approximately 20 per cent.) discharged themselves. The fact that 80 per cent. did not discharge themselves is probably due to the presence of the other tissues of the tentacle preventing the access of the water, for in similar experiments with nematocysts from a ceras of an Æolid, the whole lot were discharged when washed out with water.

These facts seem to show that the discharge of a nematocyst is due to osmosis. The capsule apparently contains a solution of such a strength that it takes up water from such a weak solution as sea water, but not from the protoplasm of the nematocytes, or the fluids in the alimentary canal of Æolids, or from any of the other solutions mentioned above.

This hypothesis does away with the necessity of supposing the capsule wall to be impermeable, and so avoids Lendenfeld's first objection. As regards the second objection, it must be remembered that for a stain to reach an undischarged nematocyst it must pass through the protoplasm of the nematocyte; it diffuses into the layer of liquid immediately surrounding the nematocyst without appreciably altering the degree of concentration, therefore, without upsetting the balance between the liquids within and without the capsule, so that by diffusion in both directions the stain can enter the capsule without causing discharge. This applies to intra-vitam staining in Cœlenterates; fixing reagents probably so alter both capsule contents and protoplasm, and perhaps also capsule wall, that arguments based on the behaviour of fixed nematocysts are untrustworthy.

But though this hypothesis explains why nematocysts are not discharged while in the alimentary canal and cnidosacs of Æolids, and are discharged when extruded into the water, two other questions suggest themselves—

1. To what is the apparent immunity of Æolids towards the nematocysts of Cnidaria due?
2. How is it that we do not find in the cnidosacs a large number

of discharged nematocysts, used by their original owners in defence against the devouring Æolids ?

1. We have seen that M. Hecht considered the immunity of Æolids towards the nematocysts of Cœlenterates to be in some way due to their possession of nematocysts of their own. But, of course, when the origin of the nematocysts of Æolids is known, it is obvious that this immunity is not a result, but a necessary condition of their possession.

Boutan (7) contends that the immunity of Æolids is not absolute, and that it is due at any rate in part to the secretion of mucus and the mode of attack. He dropped a healthy *Æ. papillosa* into the middle of the tentacles of an expanded actinian; the Æolid secreted large quantities of mucus, and after a short struggle escaped, and eventually devoured the actinian. Another individual of the same species, which had just been depositing ova and had so exhausted its supply of mucus, being treated in the same way as the last, was itself devoured. A third specimen, which had also been depositing ova, was simply placed in the same vessel with an actinian, which it devoured, beginning at the base of the column.

Æ. papillosa is, of course, an actinian-eating species and so accustomed to dealing with these animals. I have found *Spurilla neapolitana* to be equally capable of escaping from the clutches of an anemone. On the other hand, a particularly large and active specimen (6 cm. long) of *R. peregrina*, a species which usually feeds on hydroids, on being dropped among the tentacles of an expanded actinian, started to crawl out, but when the actinian began to envelope it with tentacles, it drew back and writhed in the centre, secreting mucus copiously and throwing off all its cerata. After several more vain attempts at escape it remained almost motionless, and would undoubtedly have been devoured had I not removed it with a pipette. The mucus was found to be crowded with the discharged nematocysts of the anemone and a few from the cnidosacs of the Rizzolia. The cast-off cerata were also pierced with the barbed threads of many actinian nematocysts. As for the Æolid itself, its tentacles and rhinophores, the anterior processes of the foot and the whole posterior part of the same, seemed quite paralysed, and remained stiff and useless for 3 or 4 days.

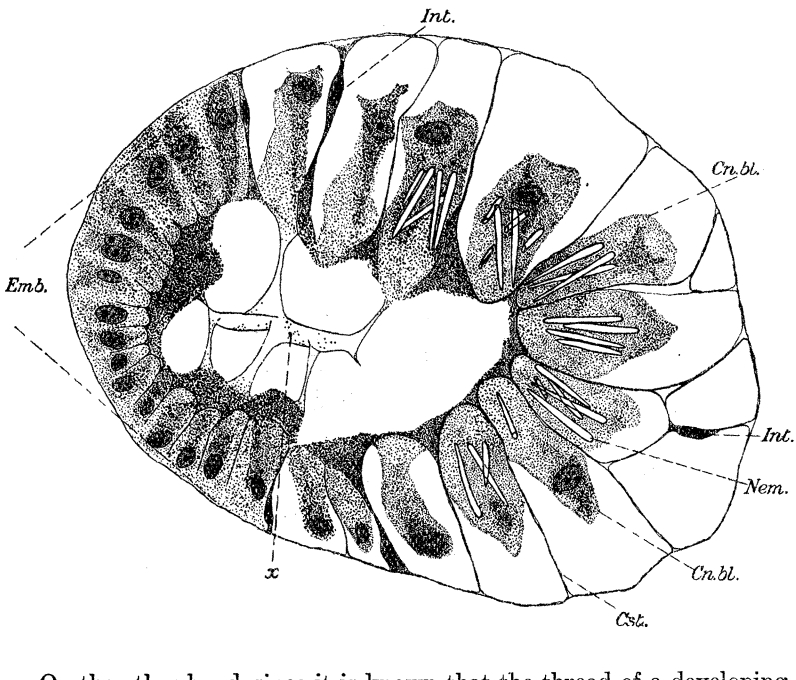
These experiments show not only that the immunity is by no means complete, but also that it depends on something besides a copious secretion of mucus.

2. The presence of only undischarged nematocysts in the cnidosacs of Æolids may be due to the nematocysts never having been discharged, or to the threads of discharged nematocysts having re-inverted by the action of the digestive fluids.

When a hydroid polyp is plucked off and examined in sea water the

small nematocysts of the tentacles usually remain undischarged; even the large nematocysts found at the base of the tentacles of many hydroids (Eudendrium) are often not discharged unless the polyps are teased up, compressed or otherwise stimulated. It is quite possible, therefore, that no attempt is made by the prey to discharge its nematocysts till it has been swallowed by the Æolid and immersed in juices of sufficient concentration to prevent the discharge. Perhaps a preliminary covering of mucus may help to delay the discharge.

FIG. 11.



On the other hand, since it is known that the thread of a developing nematocyst is formed outside the capsule and is only inverted when complete, presumably by the extraction of water from the capsule by the surrounding protoplasm, it is quite possible that the gastric juices of an Æolid may have the same effect on a discharged nematocyst.

Development and Structure of the Cnidocysts.

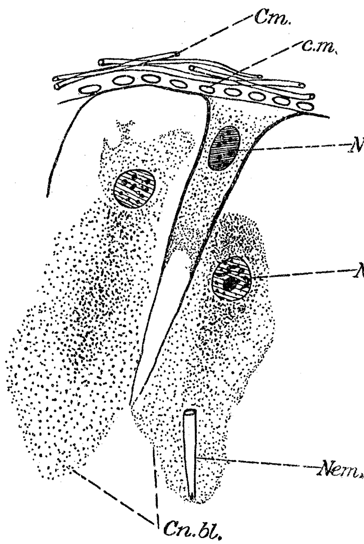
Thanks to Davenport, Hecht and Krembzow, the origin of the cnidosacs from the distal extremities of the ceratal diverticula of the gastric gland is thoroughly established, and the general outline of its development known. What observations, however, have been made on

the structure and development of the individual cnidocysts have, of course, been from the generally accepted point of view, *i.e.*, that they are nematocyst-secreting cells, instead of receptacles for fully formed foreign nematocysts.

The embryonic tissue of the cnidosac lies at the base, immediately surrounding the opening of the ciliated canal, and differentiation proceeds regularly from this point upwards, the oldest cnidocysts being next the external aperture. I have never observed a layer of embryonic cnidoblasts external to the fully formed ones.

From this embryonic zone, besides the cnidoblasts or central cells of each cnidocyst, there are developed certain interstitial cells which

FIG. 12.

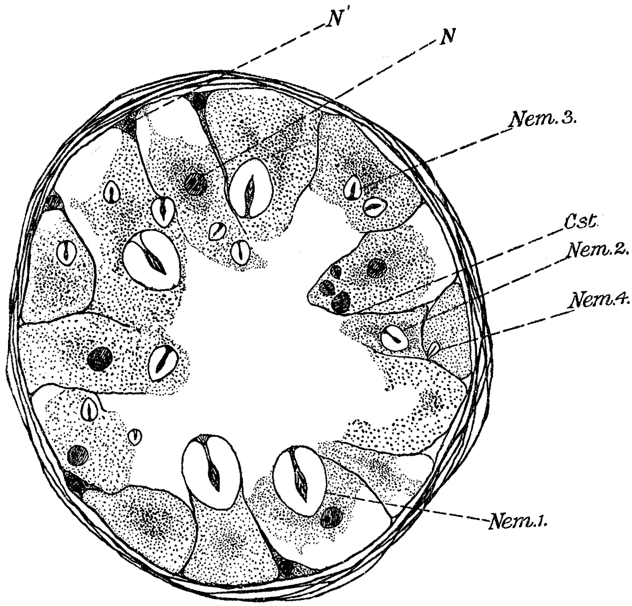


apparently take part in the secretion of the membranous cysts; these are perhaps what Herdman describes as young cnidoblasts. They lie at first between the bases of the cnidoblasts, from which they can be readily distinguished by their smaller size, and by the different staining reactions of their nuclei (fig. 12).

It is round this basal end of each cnidoblast that the membranous cyst is first secreted; the cnidoblast itself is drawn away from this point towards the lumen of the cnidosac, and does not apparently take part in the secretion of the cyst, but in the meantime ingests nematocysts at its opposite end, which remains naked and amœboid. When sufficient nematocysts have been ingested and arranged by the cnidoblast, the membranous cyst is completed, the nuclei of the intermediate cells moving up between the cnidoblasts about half way towards the lumen

of the cnidosac. When the cyst is completed both the cnidoblast and the associated intermediate cells undergo degeneration, so that in the older parts of the cnidosac each cnidocyst consists simply of a membranous bag, containing nematocysts, which are often apparently attached to its inner wall to keep them in place, and a more or less degenerate cnidoblast; while wedged between adjacent cnidocysts are found small darkly staining bodies, the remains of the intermediate cells (fig. 13).

Fig. 13.



Summary.

The facts brought forward as evidence that the nematocysts of Æolids are derived from their prey are as follows :—

1. Not only are nematocysts of Æolids and Cœlenterates identical in plan of construction and mode of discharge, but each of several distinct types occurs in both groups.
2. A single type of nematocyst does not occur uniformly throughout a species, but different individuals of the same species may have quite different nematocysts; moreover, a single individual may have nematocysts of several different types, found in as many distinct species or groups of Cœlenterates.
3. When it is known on what Cœlenterate an Æolid has recently been feeding, the nematocysts of the two are found to be

identical. Also the nematocysts from the fæces of an Æolid, which are generally admitted to be derived from their food, are always identical with at least some of the nematocysts from the cnidosacs.

4. Those Æolids (Janidæ, Fionidæ and *Calma glaucoides*) which habitually feed on animals other than Cœlenterates have no nematocysts.
5. Though several have tried, no one has succeeded in giving even a plausible account of the development of nematocysts in Æolids.
6. This view affords a satisfactory explanation of the function of the ciliated canal through which nematocysts and other indigestible bodies have been observed to pass from the gastric diverticulum to the cnidosac.
7. A repetition of Strethill Wright's experiments gave entirely confirmatory results. In one case three *R. peregrinas*, having only small pip-shaped nematocysts in their cnidosacs, were fed on *Pennaria Cavolinii*, the nematocysts of which, after a month, had almost entirely replaced the original pip-shaped ones.

In Section III the functions of the nematocysts and cnidophores of Æolids are discussed :

There is little doubt that the borrowed nematocysts are used as defensive weapons by the Æolids; they are discharged after extrusion from the cnidosacs; they are usually so arranged in the cnidocysts that the threads are shot out radially; the cerata are brightly coloured and are erected and elongated on the approach of a foreign body. The nematocysts are, however, very seldom ejected indiscriminately into the surrounding water, but usually only when the individual cerata are squeezed or plucked off.

The original and still important function of the terminal openings of the cerata is probably to allow of the escape of the nematocysts and other indigestible bodies, which, owing to the diffuse nature of the digestive cavity, it is impossible to eliminate entirely through the anus only.

Mechanism of Nematocysts.—The behaviour of nematocysts in Æolids proves that their discharge must be independent of the direct action of living tissue. The explanation most in accordance with the facts observed both under natural conditions and in experiments with various liquids and solutions, seems to be that the eversion of the nematocyst thread is due to the contents taking up water by osmosis from the surrounding sea water, but being unable to take it up from more concentrated solutions, such as the liquid surrounding the nematocysts in the Cœlenterate nematocyte or the digestive juices of Æolids.

The immunity of Æolids towards the nematocysts of Cœlenterates is not complete. It is probably due largely to the secretion of mucus, which either acts simply as a shield, or actually prevents the discharge of nematocysts.

Even without the application of mucus, the nematocysts of a hydroid are often not discharged when a polyp is plucked off the stock, so that they may be swallowed by the Æolid intact. Or the gastric fluids which are strong enough not to give up water to an undischarged nematocyst, may extract water from a discharged one and so cause the reinversion of the thread.

Development of Cnidocysts.—The cnidocysts are derived each from two or more cells of two kinds; (*a*) a single cnidoblast or central cell which ingests and arranges the nematocysts; (*b*) an undetermined number of interstitial cells which probably secrete the membranous cyst. In the adult cnidocyst both kinds of cells undergo more or less degeneration, leaving practically only a membranous bag containing nematocysts.

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EXPLANATION OF FIGURES.

Fig. 1.—Small Pip-shaped Nematocysts of Tentacles of Eudendrium from Cnidosac of *Rizzolia peregrina.* × 560.

,, 2.—Nematocysts of *Pennaria Cavolinii.* × 560.

,, 3.—Nematocysts of Tubularia. × 560.

,, 4.—Large Bean-shaped Nematocysts from Body of Polyp of Eudendrium. × 560.

,, 5.—Nematocysts from Cnidosacs of *Facelina punctata*, specimen B. × 900.

,, 6.—Large oblong Nematocysts from *Flabellina affinis.* × 560.
a. Tip of Basal portion of Thread. × 900.

,, 7.—Nematocysts of *Aiptasia variabilis.* × 560.

,, 8.—Actinian Nematocysts from Cnidosacs of *Spurilla neapolitana.* × 560.

,, 9.—Nematocysts from young Specimen of *Spurilla neapolitana.* × 560.
a. Ditto. × 900.

,, 10.—Nematocysts from Cnidosac of *Aeolidiella Alderi.* × 560.
a. From Acontia of Sagartia. *b.* From Tentacles of same.

,, 11.—Oblique Section through young Cnidosac of *Spurilla neapolitana.* Stained with Ehrlich-Biondi. × 1360.
Emb., embrionic zone at base of cnidosac; *Cn. bl.*, cnidoblast; *Nem.*, nematocyst; *Ct.*, membranous cyst; *Int.*, interstitial cells, nuclei stained greenish; *Int.'*, degenerate interstitial cell, nuclei stained red.

,, 12.—Small Portion of another Section of the same Cnidosac.
Cn. bl., cnidoblasts; *N.*, nucleus of same, stained reddish; *N'*, nucleus of interstitial cell, stained green; *l. m.*, longitudinal muscles; *c. m.*, circular muscles; *Nem.*, nematocyst.

,, 13.—Transverse Section through middle of a Cnidosac of *R. peregrina*, fed on *Pennaria Cavolinii* for one month. Some of the cnidoblasts are already surrounded by membranous cysts, while others are still ingesting nematocysts. Stained with thionin. × 800.
Nem. 1, large nematocyst of *Pen. Cavolinii* just being ingested.
Nem. 2, small ,, ,, stained reddish-violet.
Nem. 3, ,, ,, ,, ,, pale blue.
Nem. 4, ,, Eudendrium nematocyst.

FIG. 11.

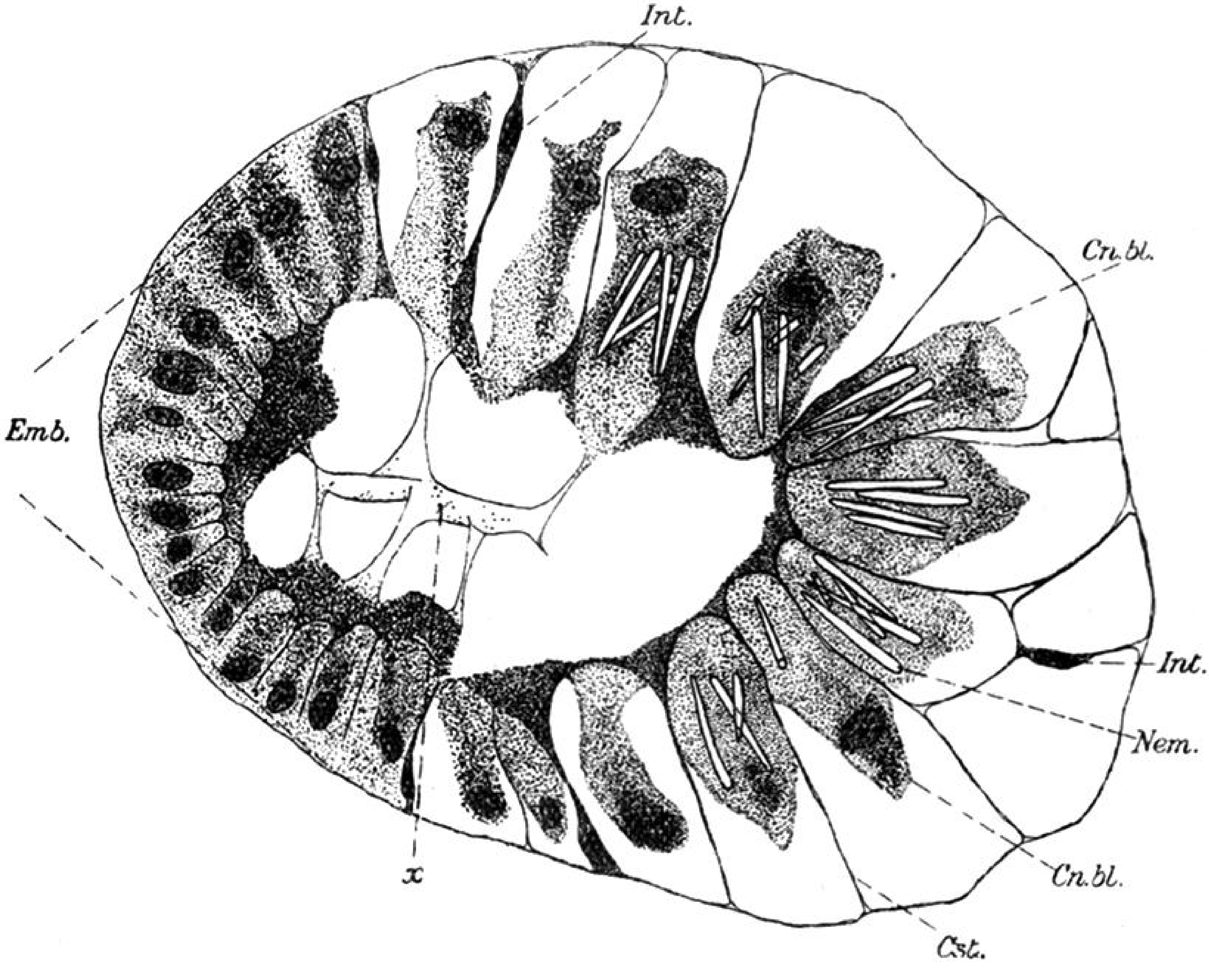

FIG. 12.

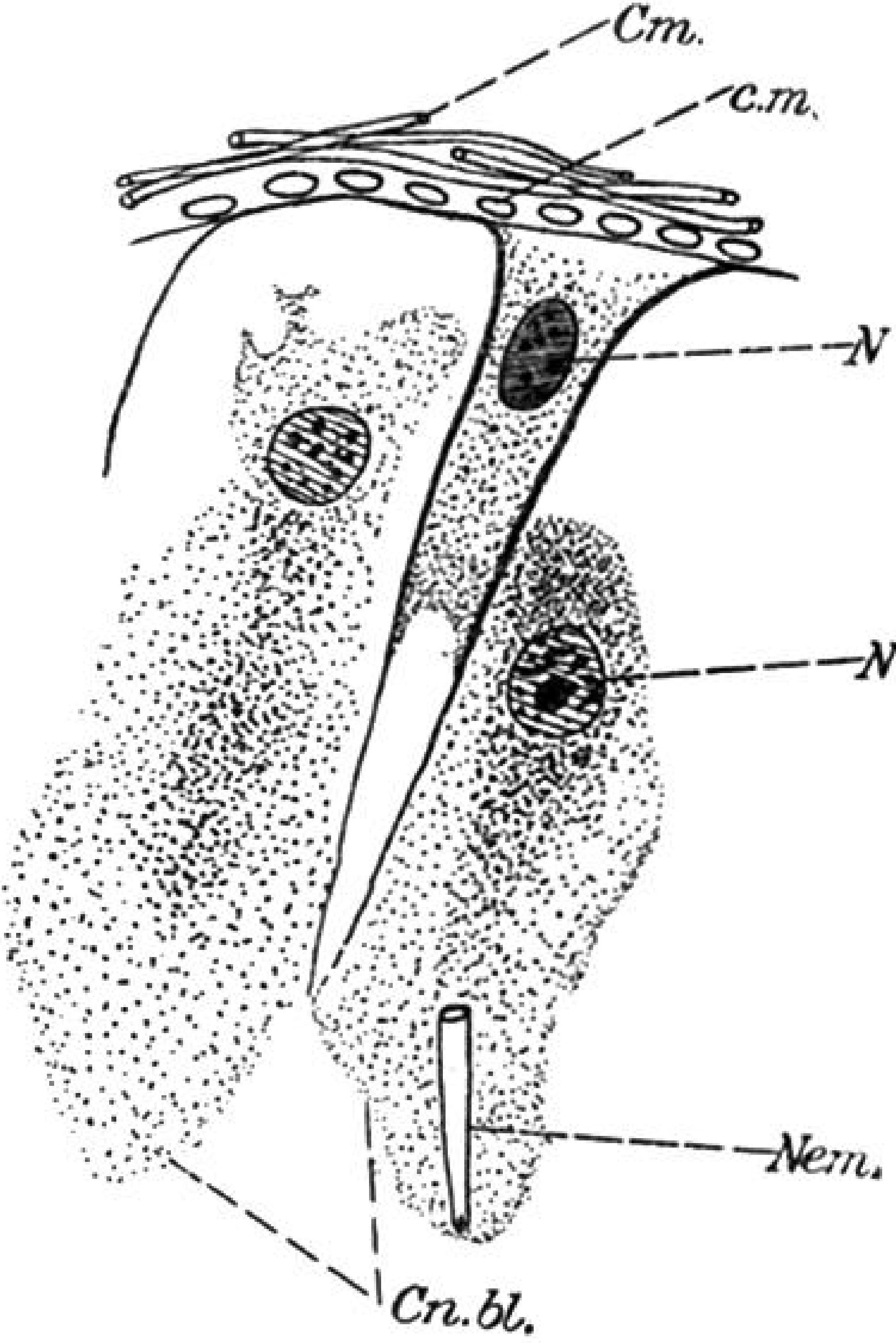

FIG. 13.